

A reappraisal of the type fossil of *Curtonotum* †*gigas* Théobald, 1937 (Diptera: Curtonotidae), a compression fossil of Early Oligocene age from Provence, France

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The fossil type of *Curtonotum* †*gigas* Théobald, 1937, from Early Oligocene deposits in Les Camoins, Provence, France, is re-evaluated and its status and placement is discussed, compared to diagnoses of the family Curtonotidae and the genus *Curtonotum* Macquart. Digitised images of the fossil are provided and these are compared in detail to digitised images of diagnostic character states of the genus *Curtonotum*, as currently recognised. Key character states required for the determination of the family are not discernable on the fossil type, due to the very poor state of preservation, and it is not possible to ascribe the species to either the Drosophilidae *sensu stricto* or Curtonotidae (as previously suggested). As the species cannot be ascribed to a family, it is treated as *insertae sedis*.

Keywords: Curtonotidae, *Curtonotum*, taxonomy, Early Oligocene, diagnoses, fossil record.

INTRODUCTION

Grimaldi & Engel (2005: 547) date the origin of the Schizophora, to which the family Curtonotidae belongs, in the latest Cretaceous to earliest Tertiary, about 65 MYA, but with their radiation exclusively in the Tertiary.

The acalyptrate family Curtonotidae represented by three extant genera worldwide, is extremely poorly represented in the fossil record (*vide* Evenhuis 2006). Only a single fossil is known; namely that of *Curtonotum* †*gigas* Théobald, 1937, a compression fossil of Early Oligocene age from Les Camoins (*ca.* 43°17'S, 5°30'E), near Marseille, Provence, France (Figure 1).

This specimen originates from outcrops of lacustrine sediments that are made up of fine laminated limestones and inter-bedded gypsum. The age of these rocks is given as Early Oligocene (*ca.* 33.9 MYA), as indicated in a recent revision of the Oligocene of Provence (J. Philip pers. comm.). These deposits are rich in fossils, especially those of insects and plants, and the descriptions of insects of several orders have previously appeared in the literature (e.g. Théobald 1937; Timon-David 1944).

Théobald (1937) provided a brief description of *C.* †*gigas* (pp. 288–289), and a line drawing of the specimen (Plate XX, fig. 8; Figure 3, this paper). As both the description and figure do not refer to, or appear to illustrate, diagnostic character states of either the family Curtonotidae or the genus *Curtonotum* Macquart, 1844, it was desirable to re-examine the specimen and assess its validity in terms of familial and generic placement.

MATERIAL AND METHODS

Images of the fossil were captured using a Canon® EOS 10D digital camera with a 50 mm macro lens and of the extant *Curtonotum tigrinum* Séguy, 1933, with a Leica® EZ4D binocular microscope with in-built digital camera. These were saved digitally and were cleaned and enhanced using the computer program Coral Draw®.

It should be noted that comparison of the fossil type of *C. †gigas* with extant species of Curtonotidae was based on the examination of digitised images captured using light microscopy only. Examination using polarising filters was not undertaken, as the poor state of preservation of the specimen did not allow such examination.

Holotype label data are quoted as they appear; a division slash (/) indicates the end of a line of print, double division slash (//) signify data on a further label. Significant supplementary or qualifying information is presented in square brackets when considered necessary. Abbreviations used in the text: 'Figure' or 'Figures' as cited in the text refers to figures cited in this paper; 'fig.' to 'figures' in other publications. NMWC = National Museum & Gallery of Wales, Cardiff, United Kingdom.

Terminology of the external morphology follows, for the most part, that of the interactive *Anatomical Atlas of Flies* (Yeates *et al.* 2004). For head bristles not defined in that work, terminology follows Barraclough (1995: 100), and abbreviations for dorso-central bristles follow Tsacas (1977: 148).

RESULTS AND DISCUSSION

PAST INTERPRETATIONS

Théobald's (1937) original French description of *C. †gigas* reads: <Insecte de petite taille, assez mal conservé, teinte brun foncé. Tête écrasée: yeux encore visibles; thorax noirâtre, fortement renflé sur le dos. Abdomen nettement séparé, forme ovale, 7 segments; pattes grêles, hanches longues, fémurs forts, velus; tibias allongés, cylindriques, munis de soies, tarses grêles. Ailes dépassant l'abdomen, nervures Sc et R accolées, se terminant avant le milieu de l'aile: on voit ensuite 4 nervures longitudinales, les 2^e et 3^e embrassant le sommet de l'aile, les nervures divergeant à peu près régulièrement, les nervures transversales ne sont pas visibles. Dim.: L du corps = 5 mm.> The English translation reads: Insect of small size, poorly conserved, dark brown colouration. Head crushed, eyes still visible; thorax blackish, strongly swollen on the back. Abdomen clearly separated, oval shaped, 7 segments; legs long and thin, hips long, femora strong, hairy; tibia elongated, cylindrical, covered with setae; tarsal segment long and thin. Wings reaching beyond abdomen, veins Sc and R fused, ending before middle of the

wing: one observes furthermore 4 longitudinal veins, the 2nd and 3rd embracing the tip of the wing, the veins diverge rather regularly, cross-veins not visible.

Dimensions: length of the body – 5 mm. (translation by Marc De Meyer).

Théobald's (1937) illustration of the fossil (reproduced here as Figure 3), exhibits a good deal of artistic licence, in terms of the accuracy of illustrated structures; especially the wing and legs.

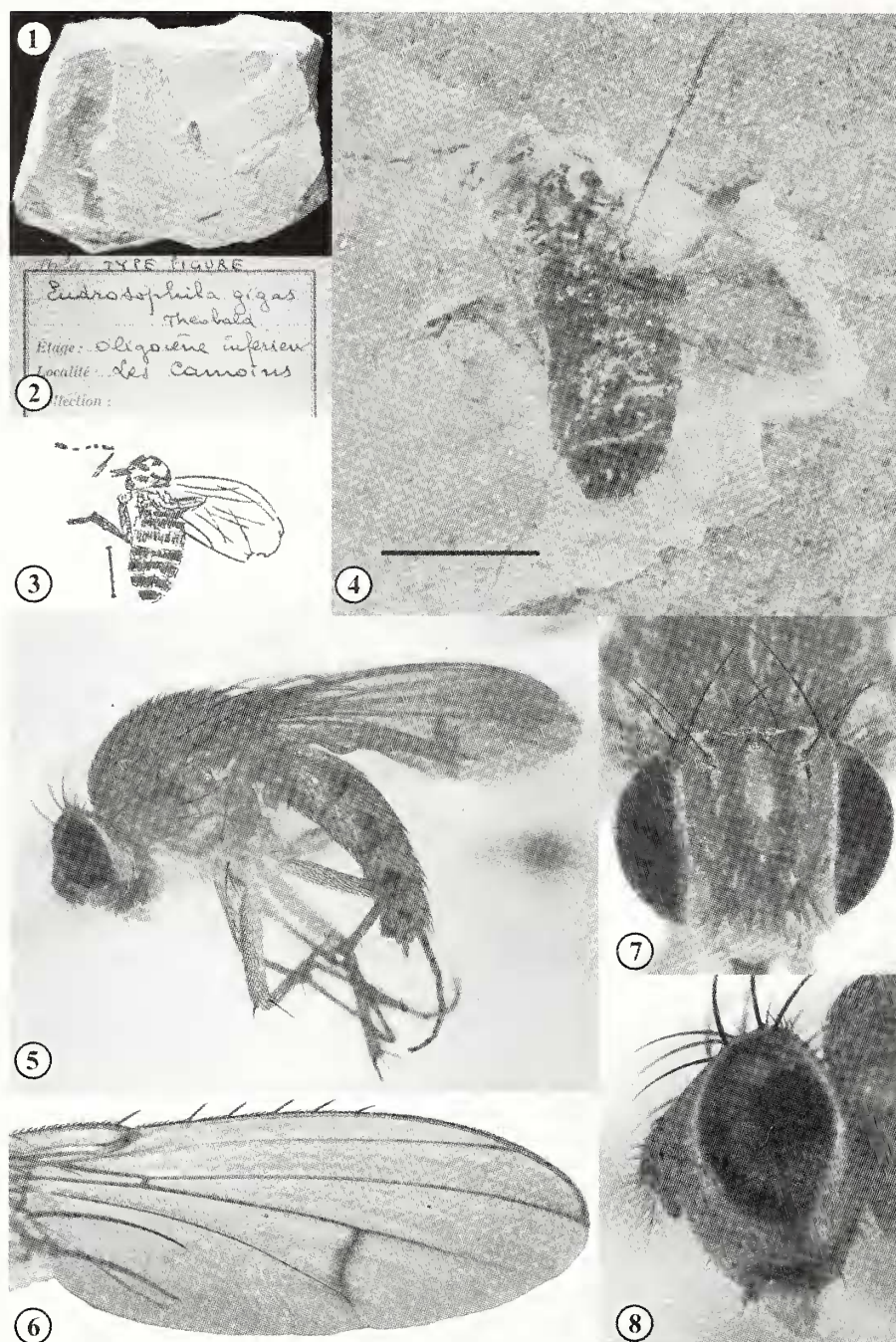
In his description Théobald (1937: 289), tentatively assigned *C. †gigas* to the genus *Curtonotum* (as “(?) g. *Cyrtonotum* MACQUART”), but further remarked that the specimen was originally identified as the [Oriental] genus *Eudrosophila* Malloch, 1924 (Drosophilidae), by Eleazar Abeille de Perrin (1843–1910), although this remained unpublished < ... cet échantillon a été déterminé *Eudrosophila gigas* par le Dr Ab. de Perrin, mais est resté inédit. Il appartient aux Drosophilidae; il se distingue facilement des Drosophiles par la taille assez considérable.> It should be noted that at the time the description appeared the Curtonotidae were regarded as a subfamily of the Drosophilidae: the Cyrtonotinae.

Théobald notes his reasons for tentatively ascribing *†gigas* to the Curtonotidae (as Cyrtonotinae), rather than to the Drosophilidae *sensu stricto*, as being the considerable size of the fossil (Curtonotidae being ‘4–5 mm’), the strongly swollen mesonotum, the simple venation, and the more elongated shape of the abdomen <Les Cyrtonotinae par contre ont une taille voisine, 4–5 millimètres; *Cyrtonotum anus* MEIGEN a aussi le mésonotum fortement renflé, la nervation de l’aile est semblable, mais l’abdomen a une forme plus allongée.> This highly superficial characterisation of both the family and the genus is clearly insufficient to ascribe the fossil specimen to either taxon by modern taxonomic standards.

In order to compare the fossil specimen of *C. †gigas* to extant representatives of the family Curtonotidae, and specifically the genus *Curtonotum*, it is first necessary to diagnose the two taxa and to list external morphological characters which in combination define them.

FAMILY: CURTONOTIDAE DUDA, 1924:

Diagnosis. The family Curtonotidae can be diagnosed as follows (based on Marshall *et al.* (in press), with amendments): Small to medium-sized (4–9 mm), distinctively robust flies, with a hump-backed, drosophilid- or heleomyzid-like form, usually greyish to yellow, often with spots, strips or irrorations on the thorax and pigment patterns on the abdomen. Arista plumose, with long dorsal and ventral rays; rays varying in number. Wing pigmentation varying from hyaline to lightly fumose (especially on r-m and dm-cu crossveins), or boldly patterned; subcosta complete, cell cup present, cells dm and bm confluent, and costa (c) with humeral and subcostal breaks. Abdomen with aedeagus enlarged, C-shaped, distiphallus anteroventrally-directed; two spermathecae present.



Figures 1–4. Early Oligocene fossil of *Curtonotum* †*gigas* Théobald from Les Camoins, Provence, France. 1, habitus of fossil in laminated limestones and inter-bedded gypsum; 2, Holotype label; 3, line drawing of *Curtonotum* †*gigas* from Théobald (1937: Plate XX, fig. 8), scale bar length unspecified, but probably 0.5 mm.; 4, detail of fossil, scale 0.5 mm. Figures 5–8. *Curtonotum tigrinum* Séguy, an extant species. 5, habitus, lateral aspect; 6, right wing, from above; 7, head, anterodorsal aspect; 8, head in profile. Not to scale.

GENUS: *CURTONOTUM* MACQUART, 1844

Type species: *Musca gibba* Fabricius, 1805 [preoccupied = *Curtonotum taeniatum* Hendel, 1913], by original designation.

Figures 5–8.

Diagnosis The genus *Curtonotum* can be diagnosed as follows (based on Tsacas (1977), with amendments): *Head* (Figures 7, 8): with two pairs of long, prominent fronto-orbital bristles, the anterior pair (or1) (those closest to antennal bases) proclinate, the posterior pair (or3) reclinate, with a minute reclinate seta (or2) positioned between them close to base of or3; frons wide in both sexes. *Thorax* (Figure 5): Scutum more-or-less hump-backed in appearance, with a pair of strong dorso-central bristles and one pair of acrostichal bristles; anepisternum with 2–3 long bristles and some short setae; one very long katepisternal bristle accompanied by a short anterior one. *Scutellum* entirely covered in hairs, with two pairs of strong marginal bristles. *Wing* (Figure 6): greyish to grey-brown infusate, dm-cu crossvein usually markedly infusate; costa (c) with humeral and subcostal breaks, and with a variable number of prominent costal spines beyond R₁ longer and stronger than adjacent vestiture. *Legs*: all tibiae with preapical dorsal bristles; forefemur with row of short, but strong spinules along distal half or third, variable in number. *Abdomen* (Figure 5): long, cylindrical, generally pale in colour with brown spots or T-shaped inverted lateral markings. Basiphallus and distiphallus fused and asymmetrical. Spermathecae flattened, short and obclavate with a folded or rugose surface or long, tubular and studded with protuberances.

MATERIAL EXAMINED

Type material examined:

Curtonotum †*gigas* Théobald, 1937. Holotype (unsexed): “Th24 TYPE FIGURE / *Eudrosophila gigas* / Theobald / Étage: Oligocène inferieur / Localité: Les Camoins / Collection: [hand-written & printed with black border; *vide* Figure 2] // 926 Th 24 Type figure / *Eudrosophila gigas* / CYRTONOTUM Theobald / Étage: Oligocène inf. / Localité: Les Camoins / Collection: [hand-written & printed]” // same except: “1613 926” [red disc in top right hand corner] (Museum de Paléontologie de Provence, Université de Provence, France).

Comparative material examined:

Curtonotum tigrinum Séguy, 1933. 1♂, 1♀, N. Nigeria, River Bagel at crossing of Bauchi-Dass road, 3.iv.1990, J.C. Deeming, roosting in moist cave in bank of dry river, NMW.Z.1981–001 (NMWC).

RE-INTERPRETATION AND COMPARISON

Given the incomplete structure of the fossil and the very poor state of preservation, it is only possible to study a limited number of structures of the external morphology, regarded as diagnostic for the family and genus; these being the wing, abdomen, foreleg and hindleg.

The head is either flattened beyond recognition or is entirely missing, and what was regarded by Théobald as the crushed head may, in fact, be derived from thoracic fragmentation. The absence of the head precludes examination of key character states diagnostic for the family Curtonotidae and the genus *Curtonotum*, such as frons width, number and arrangement of fronto-orbital bristles (Figure 7), and the arista (to assess the presence and degree of plumosity of the upper and lower surfaces) (Figure 8). The absence of the head is the single most important limiting factor to the correct determination of the specimen.

Due to excessive compression, the thorax is too flattened and expanded to make a true assessment of the degree of convexity as it would have appeared in an unaltered state (e.g. as in Figure 5). Such a character is, in isolation, of little or no taxonomic value, as a hump-backed appearance is apparent in numerous species of Diptera in various families, including the closely-related drosophiloid families Diastatidae, Campichoetidae and some Drosophilidae. Identification is further hampered by the dorso-central and acrostichal bristles being obscured and the chaetotaxy and setation of the anepisternum and katepisternum not being visible (bristles evident in Figure 5).

As far as the visible legs are concerned, there is no evidence of preapical dorsal bristles, and the forefemur does not appear to exhibit the row of short, strong spinules diagnostic for the genus *Curtonotum*. This, however, is probably again due to poor preservation.

The writer has been unable to accurately assess the number of abdominal segments, either from Théobald's original fig. 8 (Figure 3, this paper), or from the digital images of the specimen (Figure 4). Théobald's interpretation of a tubular abdomen clearly holds no taxonomic value, even were such a shape discernable from the fossil, which it is not. The abdomen appears, in fact, to be shortened and robust rather than 'tubular'.

The most significant external morphological structure in determining the correct placement of the fossil at familial and generic level (other than the head discussed above), is the venation and arrangement of bristles along the costa (c) of the wing (*vide* Figure 6). Théobald's original fig. 8 (Figure 3, this paper), illustrates a more-or-less complete pair of wings with an excavated missing section at the posterior apical lobe of the 'upper' wing. The venation is indicated as a series of unstructured lines, clearly unrelated to the actual arrangement on the fossil specimen. Re-examination of the fossil has revealed that the wing is, in fact, folded back upon itself and broken, and that the

costal margin beyond R_1 , which is so critical in determining the presence of conspicuous costal spines, is visible posteriorly rather than anteriorly. There are clearly no spines along the costa, either before or after R_1 . Cells cup, dm and bm are not visible, so it is not possible to ascribe the species to the Curtonotidae based on these characters.

It must be concluded, therefore, that although many external morphological character states are not visible on the specimen, the clear absence of conspicuous spines on the costa precludes the species from placement in *Curtonotum* (as currently defined). As the head and basal section of the wing are not present on the fossil, it is not possible to ascribe it to a family with any degree of certainty. Thus there is no evidence to support Théobald's familial or generic placement within the Curtonotidae. The specimen and species must, therefore, be treated as *insertae sedis*. It can only be hoped that more suitable fossils of the family Curtonotidae come to light in the future (especially amber-preserved specimens) and that they will elucidate our understanding of the evolutionary history of the family.

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REFERENCES

- BARRACLOUGH, D.A. 1995. An illustrated identification key to the acalyptrate fly families (Diptera: Schizophora) occurring in southern Africa. *Annals of the Natal Museum* **36**: 97–133.
- DUDA, O. 1924. Beitrag zur Systematik der Drosophiliden unter besonderer Berücksichtigung der paläarktischen und orientalischen Arten (Dipteren). *Archiv für Naturgeschichte* (A) **90** (3): 172–234.
- EVENHUIS, N.L. 2006. *Catalogue of the fossil flies of the world (Insecta: Diptera)*. On-line version, available at: <http://hbs.bishopmuseum.org/fossileat/fosscurto.html>

- FABRICIUS, J.C. 1805. *Systema antliatorum secundum ordines, genera, species adiectis synonymis, locis, observationibus, descriptionibus*. Brunsvigae [=Brunswick], xiv + [xv-xvi] + 1-372 pp. + errata.
- GRIMALDI, D. & ENGEL, M.S. 2005. *Evolution of the insects*. Cambridge University Press, Cambridge, xv + 1-755 pp.
- HENDEL, F. 1913. Neue amerikanische Diptera. 1. Beitrag. *Deutsche entomologische Zeitschrift* 1913: 617-636.
- MACQUART, J. [1844]. *Diptères exotiques nouveaux ou peu connus. Tome deuxième.-3^e partie*. N.E. Roret, Paris, 5-304 pp.
- MALLOCH, J.R. 1924. Two Drosophilidae from Coimbatore. *Memoirs of the Department of Agriculture in India. Entomological series* 8: 63-65.
- MARSHALL, S.A., KIRK-SPRIGGS, A.H. & KLYMKO, J. (in press). Curtonotidae. In BROWN, B.V. (ed.). *Manual of Central American Diptera*.
- SÉGUY, E. 1933. Contributions à l'étude de la faune du Mozambique. Voyage de M.P. Lesne (1928-1929). 13^e note. - Diptères (2^e partie). *Memórias e estudos do Museu zoológico da Universidade de Coimbra* 67: 5-80.
- THÉOBALD, N. 1937. *Les insectes fossiles des terrains oligocènes de France*. G. Thomas, Nancy, 473 + [1] p. (pp. 228-229).
- TIMON-DAVID, J. 1944. Insectes fossiles de l'Oligocene inférieur des Camoins (Bassin de Marseille), Part 1. *Bulletin de la Société entomologique de France* 48 (1943): 128-134.
- TSACAS, L. 1977. Les Curtonotidae (Diptera) de l'Afrique: 1. Le genre *Curtonotum* Macquart. *Annals of the Natal Museum* 23: 145-171.
- YEATES, D.K., HASTINGS, A., HAMILTON, J.R., COLLESS, D.H., LAMBKIN, C.L., BICKEL, D., MCALPINE, D.K., SCHNEIDER, M.A., DANIELS, G. & CRANSTON, P. 2004. *Anatomical atlas of flies*. CSIRO, Canberra, Australia. Available at: <http://www.ento.csiro.au/biology/fly/fly.html#>

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